A New Interpretation of Affinities within the Anopheles hyrcanus Complex of Southeast Asia

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ABSTRACT

A new interpretation, based on an analysis of characters from all life stages, is proposed to explain the affinities within the Southeast Asian Anopheles hyrcanus complex. The position of each species is discussed: argyropus and sinensis are retained separately, while the nigerrimus subgroup is proposed for nigerrimus, pursati, indiensis and pseudosinensis, and the lesteri subgroup is proposed for lesteri lesteri, lesteri paraliae, crawfordi and peditaeniatus. Other Oriental anophelines which may belong to the hyrcanus complex are also discussed.

INTRODUCTION

In 1953, after at least 14 years of study, Reid published his revision, "The Anopheles hyrcanus Group in South-East Asia." This publication clarified the specific identities involved in this complex and gave public health personnel and taxonomists in Southeast Asia some long needed tools with which disease vector problems could be tackled and solved. Included was a lengthy discussion of relationships, which coupled with later works (Reid 1963, 1968) make up his interpretation of the affinities within the complex.

During the present study (1967 to present) thousands of specimens of this complex were examined. This work was conducted in Hong Kong (New Territories), the Philippines, Thailand and the U.S., under the auspices of the SEATO Medical Research Laboratory, Bangkok, and the Southeast Asia Mosquito Project, Smithsonian Institution, Washington. Among the material in the U.S. National Museum were numerous specimens with associated skins, including some identified by Reid. This study revealed an interpretation of affinity different from that of Reid (1953, 1963 & 1968). The interpretation as proposed here, best explains the affinities within the Southeast Asia hyrcanus complex and hopefully will stimulate further work on the Oriental members of the complex.

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REVIEW

Prior to 1953, workers on the Southeast Asian fauna had described a number of varieties of Anopheles hyrcanus (Pallas) which were usually lumped under two names, i.e. hyrcanus var. nigerrimus Giles, and hyrcanus var. sinensis Weidemann (Christophers 1933, Crawford 1938). This variety concept lasted beyond World War II (Puri, 1949), until Reid recognized 8 separate species from within the 2 varieties: argyropus (Swellengrebel), crawfordi Reid, indiensis Theobald, lesteri Baisas and Hu, nigerrimus Giles, peditaeniatus (Leicester), pseudosinensis Baisas and Hu and sinensis Weidemann. He also described a ninth species, but did not name it other than calling it species "D_2 near nigerrimus." He later (1963) found this species equivalent to pursati Laveran, and resurrected pursati from synonymy under nigerrimus. Meanwhile, Sandosham (1959) had named paraliae, a new subspecies of lesteri, based on differences noted by Reid (1953) between the Philippine and Malayan forms of lesteri.

To date there are 14 taxa in the Orient which possibly belong to this complex. The following 4 species may be Palearctic representatives and are not included here due to lack of specimens:

Anopheles (An.) kweiyangensis Yao & Wu, 1944
" " pullus Yamada, 1937
" " sineroides Yamada, 1924
" " yatsushiroensis Miyazaki, 1951

The remaining 10 taxa are the true Southeast Asian members (Reid, 1968), and the basis for this interpretation:

Anopheles (An.) argyropus (Swellengrebel), 1914
" " crawfordi Reid, 1953
" " indiensis Theobald, 1901
" " lesteri lesteri Baisas & Hu, 1936
" " lesteri paraliae Sandosham, 1959
" " nigerrimus Giles, 1900
" " peditaeniatus (Leicester), 1908
" " pseudosinensis Baisas & Hu, 1936
" " pursati Laveran, 1902
" " sinensis Weidemann, 1828

SUMMATION OF REID'S CONCLUSIONS

Reid's (1953, 1963 & 1968) interpretations can be visualized best by the following species groupings and brief explanations:

argyropus	sinensis	indiensis	crawfordi
peditaeniatus	pseudosinensis		lesteri lesteri
	nigerrimus		lesteri paraliae
	pursati		

Anopheles argyropus is related to the African An. coustani species complex, and is also probably related to peditaeniatus. Anopheles sinensis and nigerrimus are related, and the isolated Philippine species, pseudosinensis, has characters intermediate between those 2 species, although

it is more closely related to nigerrimus than sinensis. Anopheles pursati is closely related to nigerrimus. Anopheles indiensis is is somewhat intermediate between crawfordi and nigerrimus. Although crawfordi is superficially like sinensis, it is more closely related to lesteri.

SELECTION OF CHARACTERS

Some of the characters used previously were found too variable for use in this interpretation; they are: (A) all linear measurements; (B) tarsal banding; (C) scale pattern on female palpi; (D) presence or absence of a fringe spot on vein Cu_2; and (E) color designations for pale wing scales. Linear measurements are subject to a wide range of variation due to extrinsic and intrinsic stimuli (Clements, 1963), and the analysis of such variation should be conducted with extreme care (Gould, 1966; Mayr, 1969). Mayr (1969) considers linear measurements and other highly variable characters of low weight value and to be avoided if possible. Those characters which were finally selected segregate the included species into well defined, related subgroups, while exhibiting a high degree of consistency and non-functional correlation. These are attributes of characters worthy of high weight in the analysis of similarity (Mayr, 1969).

CHARACTER DEFINITION

1. Number of leaflet pairs on the male aedeagus. The aedeagus of Anopheles is bilaterally symmetrical and when split (flat mounts) nearly always exhibits an identical number of leaflets (when present) on each side.

2. Presence or absence of a basal pale band on the third palpal segment of males. Self explanatory, but not to be confused with a mesal-longitudinal pale stripe or scattered pale scales.

3. Presence or absence of pale scales on the basal 1/3 of the male costa. May be in the form of scattered pale scales and/or a distinct costal spot.

4. Presence or absence of a tuft of scales on the humeral cross vein. Tuft defined as 4 or more scales, as compared with no scales or rarely 1-2 scales.

5. Structural modification of the pupal trumpet rim and pinna. Aside from the usual thin uniform rim, the following 2 modifications are used: (A) thickened areas on the rim with a saw-tooth like edge, and (B) vertical wrinkles on the outer wall of the pinna. These modifications are constant structural differences found in certain species in the Myzorhynchus series.

6. Number of branches on pupal abdominal seta 5-V. Self explanatory.

7. Number of branches on larval head seta 8-C. Self explanatory.

8. Number of long pecten teeth on larval pecten plate. Self explanatory.

9. Egg deck width. A ratio that varies from wide (approximately 1/3-1/2 width of egg), moderate 1/7-1/6 width of egg), narrow 1/10 width of egg) to very narrow (1/20 width of egg). Widths are not known for those eggs described with split decks.

The reader should consult Reid (1968) for illustrations of these characters.

CHARACTER VALUE

The characters represent all 4 life stages and both sexes of the adult. As pointed out by Mayr (1969), if an analysis of similarity has been conducted properly, equivalent affinities should be demonstrable in all the life stages.

All characters defined have been used previously, but not on the level proposed herein. Character 1 was previously used on the species level, and Reid & Knight (1961) found the presence or absence of aedeagal leaflets very significant in the separation of species groups in the Anopheles series. Characters 2-4 and 6-9 were all previously important characters at the specific level. Character 5 as defined, has only been used on the species level; however, more basic structural differences in the pupal trumpet were used by Reid & Knight (1961) to divide the subgenus Anopheles into the Laticorn and Angusticorn Sections.

RESULTS

As is often the case in closely related species or groups of species, many similarities exhibited in a single life stage or single sex are often found to be superficial when examined in the light of characters on the remaining life stages. This is exactly the situation found in the females of this complex. Only one female character was useful in this analysis, and while others may eventually be found, this analysis was possible only after studying all the life stages.

Tabulation of the selected characters (Table 1) illustrates the consistency and correlation of the characters by the segregation of the included species as follows:

argyropus	nigerrimus	sinensis	lesteri lesteri
	pursati		lesteri paraliae
	indiensis		crawfordi
	pseudosinensis		peditaeniatus

Anopheles argyropus and sinensis are separated because their characters do not agree well with the other species or each other; otherwise, the majority of characters separate the remaining species into 2 well defined categories. The first category (nigerrimus subgroup) is generally characterized by: (1) a low number (2-3) pairs of aedeagal leaflets; (2) a pale basal band on the male third palpal segment; (3) presence of pale scales on the base of the male costa; (4) a tuft of scales on the

humeral cross vein; (5) a thin, uniform rim on the pupal trumpet; (6) a large number of branches (30 or more) on pupal seta 5-V; (7) a large number of branches (11 or more) on larval seta 8-C; and (8) 7 or less long pecten teeth on the larval pecten plate. The egg character is not presently applicable at this point (see later discussion). The second category (lesteri subgroup) is generally characterized by: (1) a high number (4 or more) pairs of aedeagal leaflets; (2) absence of a pale basal band on the male third palpal segment; (3) base of the male costa entirely dark scaled; (4) humeral cross vein bare or rarely with 1-2 scales; (5) rim of pupal trumpet with thickened areas and saw-tooth edge; (6) fewer branches (40 or less) on pupal seta 5-V; (7) fewer branches (12 or less) on larval seta 8-C; (8) 7 or more long pecten teeth on the larval pecten plate; and (9) generally narrower egg deck width. Exceptions to some of these generalizations are found in pseudosinensis, crawfordi and peditaeniatus and will be discussed later.

As can be seen, this interpretation differs from Reid's by 4 major changes: (1) separating peditaeniatus from argyropus and placing it in the lesteri subgroup; (2) determining argyropus to be separate, but more closely related to nigerrimus than peditaeniatus; (3) moving sinensis away from a close relationship with nigerrimus and placing it separate, but possibly intermediate between the nigerrimus and lesteri subgroups; and (4) removing indiensis from an intermediate position between crawfordi and nigerrimus and placing it in the nigerrimus subgroup.

DISCUSSION

NIGERRIMUS SUBGROUP: The first group of species consists of nigerrimus, pursati, indiensis and pseudosinensis, and is called the nigerrimus subgroup because of the more central position this species occupies in the subgroup. The above order in listing the remaining members of the subgroup is arbitrary and not meant to imply relationship. The characters used by Reid to associate indiensis with crawfordi appear superficial, for although the branching on pupal seta 5-V and scaling on the base of the male costa is similar, the remaining characters are dissimilar. Anopheles pseudosinensis, which is restricted to the Philippines, has few branches on pupal seta 5-V and larval seta 8-C, like those found on sinensis and the members of the other subgroup. This similarity may be actual or superficial; nevertheless, pseudosinensis is definitely misnamed, for as Reid (1953) pointed out, it is most closely related to nigerrimus.

The apparent disparity found in the types of egg decks in the nigerrimus subgroup might cause considerable concern if studies such as those of Otsuru and Ohmori (1960) were not available for review. These authors found extensive variation in the eggs of sinensis, lesteri lesteri, sineroides and yatsushiroensis between summer and late autumn in Japan. This variation ranged from the single long deck form to a distinct split deck form in all 4 species. Of the 4 species in the nigerrimus subgroup, the eggs of nigerrimus and pseudosinensis are described with a single long deck, while eggs of pursati and indiensis are described with split decks. The apparent disparity in these 2 types of egg decks may not be real, but reflect a limited number of

eggs previously studied without regard for seasonal variation. All members of the nigerrimus subgroup are found in countries with distinct wet and dry seasons, which may induce egg variation similar to that found in Japan. Much more work is needed on the eggs of all members of this complex.

There may be additional species or subspecies belonging to this subgroup. Reid (1963 & 1968) considered An. minutus Theobald, a synonym of nigerrimus for convenience only and commented that it may actually represent another distinct species. This Pakistan form possesses a long basal dark mark on vein Cu and broad hind tarsal pale bands, characters usually associated with the nigerrimus subgroup. Further work in Indonesia may also reveal that venhuisi Bonne-Wepster, currently a synonym of nigerrimus, is a valid name. Currently, there are no confirmed records of this subgroup north or northeast of Vietnam, and there are many areas in its wide distribution from West India-Pakistan to the Philippines where additional study may reveal cryptic related species.

LESTERI SUBGROUP: The lesteri subgroup consists of lesteri lesteri, lesteri paraliae, crawfordi and peditaeniatus. Although peditaeniatus has date priority over the other names it does not occupy a central position in the subgroup. Currently, paraliae is listed as a subspecies of lesteri, but may deserve specific status. The nominate subspecies is currently considered present in China, Japan, the Ryukyus and most of the major islands in the Philippines (Type Locality), while paraliae is currently known from Malaysia (East and West), Singapore and Thailand. Areas of overlap would supposedly occur where Sabah joins with the Philippine Palawan Island chain on the North, and where it joins with the Sulu archipelago on the East. There are currently no confirmed records of the nominate subspecies from Palawan Island or the western end of the Sulu Island chain. The subspecies, paraliae, is definitely recorded from Sabah, but not from areas adjacent to the above island chains. Much more collecting is needed in these areas before this problem can be solved.

Anopheles crawfordi possesses 2 characters like those of the nigerrimus subgroup: (1) pale scales on the basal 1/3 of the male costa, and (2) more numerous branches on pupal seta 5-V. The number of long pecten teeth on the larva is somewhat intermediate between the 2 subgroups. However, all the remaining characters clearly place crawfordi in the lesteri subgroup. One inconsistency remains concerning a primary character. Reid (1953 & 1968) described the male of crawfordi as sometimes having a small pale band at the base of palpal segment 3. None of the males the author has examined of this species from both Thailand and Malaya exhibit even a trace of a basal pale band on that segment. Further collections will probably resolve this inconsistency.

Besides a difference in egg deck width, at least 3 adult characters are present on peditaeniatus that are distinct from the other members of the subgroup. This species has hind tarsal pale bands of variable size (see below), but is the only member of the subgroup that frequently exhibits broad hind tarsal bands. The wing of peditaeniatus usually has extensive pale scaling on vein R-R_1 and a long basal dark mark on vein Cu, both characters, usually lacking on the other members.

There are probably other species which belong to this subgroup, particularly in China. Feng (1964) described the egg of kweiyangensis and 4 egg types under the name "sinensis." The former species is very similar to sineroides from Japan, Korea and northern China (Reid, 1963). Of the "sinensis" eggs, one was the "broad decked egg type" which is probably equivalent to sinensis. Another, the "medium decked egg type" is probably equivalent to peditaeniatus. The adult description given by Feng in association with this latter egg type fits several adults examined in the USNM from Fukien, Kweichow and Yunnan provinces, China. These adults appear identical to and have narrow hind tarsal bands like specimens of peditaeniatus from Assam, other parts of India and northern Thailand. They all have white to silvery-white scales on the remigium, no scales on the humeral cross vein, a long basal dark mark on vein Cu and numerous pale scales on vein R-R_1, which are indicative of peditaeniatus. The abdomen and legs of the single male are missing, but the palps do not have a pale basal band on segment 3. Further discussions on the variations found in peditaeniatus hind tarsal banding can be found in Reid (1963 & 1968). The 2 remaining egg types described by Feng, "narrow decked egg type" and "extremely narrow decked egg type" probably represent members of the lesteri subgroup. In fact, one probably is equivalent to the species found in southern China, Japan and the Ryukyu Islands, which is currently considered conspecific with lesteri lesteri of the Philippines. This latter Chinese species may actually be distinct from that of the Philippines and certainly deserves more attention since Ho et al. (1962) demonstrated that it, not sinensis, is the major vector of malaria pathogens in the Yangtze valley of China.

This subgroup has a distribution from Japan and China south through the Indonesian chain into the Philippines and west into India. Only one species, peditaeniatus, extends into India south and west of Assam and Bangladesh. This species and sinensis apparently have the widest distributions of all the members of the Southeast Asian hyrcanus complex. Since both species prefer warm shallow water for oviposition, the spread of rice cultivation across Southeast Asia may be directly responsible for their wide distributions.

ARGYROPUS: The complement of characters found on argyropus are quite distinct. Actually, argyropus has 4 of 9 characters (Table 1) similar to the nigerrimus subgroup: (1) aedeagal leaflets; (2) scale tuft on humeral cross vein; (3) numerous branches on pupal seta 5-V; and (4) numerous branches on larval seta 8-C. Three characters are more like those of sinensis and the lesteri subgroup: (1) male palpal segment 3 without basal pale band; (2) basal 1/3 of male costa dark scaled; and (3) very narrow egg deck (but see below). One character, i.e. the number of long larval pecten teeth, is intermediate between the 2 subgroups. The remaining character, wrinkles on the pupal trumpet, is unique in this complex, but is found elsewhere in the An. coustani complex in Africa. Reid (1968) presented a number of characters which point to a relationship between argyropus and this African complex. The very narrow decked egg of argyropus, besides looking similar to those of the lesteri subgroup (except peditaeniatus), is very similar to those illustrated in Gillies and de Meillon (1968) for An. tenebrosus and ziemanni, both members of the coustani complex.

Reid (1953 & 1968) proposed that argyropus shows its closest relationship to the SE Asian hyrcanus complex through peditaeniatus and based this in part, on broad hind tarsal pale bands, female palpal banding and wing scale color. These characters were found too variable to use in the present study. The 2 remaining, and strongest supporting characters for Reid's proposal, are the long refractile margin on the pupal paddle and the spine-like seta 9-VIII on the pupae. However, only 2 adult characters in Table 1 support this proposal, while the 2 pupal characters used in Table 1 contradict this similarity; consequently, Reid's pupal characters probably reflect superficial similarities. On the other hand, argyropus is more closely related to nigerrimus than peditaeniatus by 4 characters present in Table 1, and the following additional characters: (1) dark scaled remigium; (2) narrow pale band on mid tarsomere 3; (3) larval seta 4-M with stiff, erect branches; and (4) larval seta 3-C with 70 or more branches. Besides a probable relationship with the African coustani complex, argyropus appears to be more closely related to nigerrimus and the nigerrimus subgroup than the other species in the SE Asian hyrcanus complex.

SINENSIS: Interpreting the position of sinensis in this analysis is difficult. Actually, sinensis shares 4 of the 9 Table characters with the lesteri subgroup: (1) aedeagus leaflets; (2) male palpal segment 3 without basal pale band; (3) few branches on pupal seta 5-V; and (4) number of long larval pecten teeth. Another character, the thin pupal trumpet rim, is like the nigerrimus subgroup, while the wide deck on the egg is unique in the SE Asian hyrcanus complex. The remaining 3 characters are intermediate between the 2 subgroups. The first of these, pale scales on the base of the male costa, is variable, with true SE Asian specimens dark scaled while specimens from the more northern latitudes (China) exhibit numerous pale scales in this area, much like An. hyrcanus (Pallas). The second character, presence of a scale tuft on the humeral cross vein, could be confusing. Anopheles sinensis normally has 3-6 small scales in this area, rarely less, but these scales are not large and do not form a tuft as on argyropus and the nigerrimus subgroup. The number of branches on larval seta 8-C is the third intermediate character. Although sinensis is most closely related to the lesteri subgroup, affinities with the nigerrimus subgroup are also evident; consequently, sinensis is best assigned to an isolated intermediate position. However, it is also possible that sinensis is related to the Palearctic hyrcanus complex and links the lesteri subgroup to that complex. The whole problem of sinensis and its affinities is an enigma which must be solved if we are to understand the relationships of the Palearctic and the Southeast Asian hyrcanus complexes. Reid (1968) in speaking about the distribution of the Mediterranean and Near East (Palearctic) species of the hyrcanus complex in relation to the Oriental species noted that, "Meantime it is convenient to assume that none of them, including hyrcanus itself, occurs in the Oriental region, where a different set of names is in use, and where the taxonomy of the group is more advanced, though much still remains to be done." Unfortunately, the resolution of the sinensis problem must necessarily involve both components of the complex, for the distribution of hyrcanus extends north and east into Mongolia, Manchuria and Siberia (Bates et al., 1949), while sinensis is known from northern China and Korea. Reid (1953) discussed 2 forms of sinensis from northern China, calling the more northern form the Palearctic form. The identity of the northern species called

hyrcanus and the 2 Chinese sinensis forms needs clarification. Resolution of this problem should be most enlightening, and help demonstrate the origin of the Southeast Asian species.

SUMMARY

The major purpose of this interpretation is to establish a means by which the Oriental species of the hyrcanus complex can be analyzed by a given set of characters and segregated into supraspecies taxa. Some workers may feel the introduction of subgroup names unnecessary; however, such names hold no taxonomic status and serve as useful tools in such analyses. Hopefully, these subgroups will serve as nuclei in future work with the other members of the hyrcanus complex. The basic design of this analysis should remain useful, although the groupings may eventually change due to the examination of additional material.

Much work is still needed on the Chinese and Indian faunas and the Palearctic forms of species such as lesteri and sinensis. The following species are all apparently related to the Southeast Asian hyrcanus complex but need further study: kweiyangensis (China), pullus (Korea), sineroides (China, Japan and Korea) and yatsushiroensis (Japan). Obviously, the insertion of these species into this analysis requires the detailed study of all the life stages.

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TABLE 1

Species	ADULT				PUPAL		LARVAL		EGG
	Pairs of aedeagus leaflets	Pale band on ♂ palpal seg.3	Pale scales on base of ♂ costa	Scales on humeral cross vein	Trumpet structure	Branches on pupal seta 5-V	Branches on larval seta 8-C	No. long pecten teeth	Deck width
argyropus	2	no	no	tuft	wrinkles	50+	13-22	6-8	very narrow
nigerrimus	2-3	yes	yes	tuft	thin	40-60	12-24	4-7	moderate
pursati	2-3	yes	yes	tuft	thin	45+	12-21	5-7	split deck
indiensis	2-3	yes	yes	tuft	thin	30-50	11-21	5-7	split deck
pseudosinensis	2	yes	yes	tuft	thin	4-11	5-12	6-7	moderate
sinensis	3-6	no	no*	tuft**	thin	9-24	8-14	7-9	wide
lesteri lesteri	4-5	no	no	none or 1-2	thick saw-toothed	10-37	5-12	7-10	narrow
lesteri paraliae	4-5	no	no	none or 1-2	thick saw-toothed	12-30	5-11	7-10	narrow
crawfordi	4-7	no	yes	none or 1-2	thick saw-toothed	30-45	6-11	6-8	very narrow
peditaeniatus	4-7	no	no	none or 1-2	thick saw-toothed	14-28	4-9	7-9	moderate

* Rare in Southeast Asia; more frequent on palearctic form in China
** Not actually a tuft, but 3-6 small scales, rarely less or bare